Interchangeable sets of complementary habitat variables and target values allow for flexible, site-adapted wildlife habitat management in forest ecosystems

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Abstract

Integrating biodiversity conservation into forest management is a major goal in sustainable forestry. Hence, target values for forest structural and compositional stand characteristics are required to ensure wildlife habitats of sufficient extent and quality. Yet, the possibility to meet these targets depends on the patch conditions, notably their initial state and future trajectory. Shaped by succession, site conditions and management regime, not all forest stands can be readily converted into a particular state, which calls for flexible management prescriptions. Using the example of two forest grouse species, capercaillie and hazel grouse, we sought complementary variable combinations – with quantitative thresholds for any given crucial habitat feature – which would likewise offer suitable habitat. Habitat variables were mapped in sampling plots within occupied and non-occupied 1 km^2 grid cells distributed across three Swiss mountain regions. Generalized Linear Mixed Models (GLMM) were combined with Conditional Inference Trees (CIT) to identify species-relevant variable combinations and variable thresholds. Important features for both species were the proportion of bilberry (*Vaccinium myrtillus*) and the number of basal-branched trees, as well as a low proportion of beech (*Fagus sylvatica*) in the canopy layer. Hazel grouse additionally favoured rowans (*Sorbus aucuparia*) as feeding trees and a high percentage of herbs in the ground layer, while the presence of inner forest edges was additionally important for capercaillie. Thresholds were not clear-cut: different values applied for a particular variable depending on other, functionally similar habitat variables present at the site. By delivering information about relevance, interactions and the required amount of crucial variables, we provide alternative options for flexible species habitat management which allows accounting for the prevailing stand conditions.

Zusammenfassung

Die Integration von Naturschutzzielsetzungen in die Waldbewirtschaftung ist wesentliches Ziel einer nachhaltigen Waldwirtschaft. Um Wildtierlebensräume in ausreichendem Umfang und Qualität zu gewährleisten werden waldstrukturelle Zielwerte benötigt. Die Möglichkeit diese Zielwerte zu erreichen hängt jedoch maßgeblich von den Ausgangsbedingungen und dem Entwicklungspotential eines Waldbestandes ab. Je nach Sukzessionsstadium, Standortsbedingungen und Bewirtschaftungsform können nicht alle Bestände gleichermaßen in einen gewünschten Zustand überführt werden. Dies macht flexible Managementvorgaben erforderlich. Am Beispiel von zwei sympatrischen Raufußhuhnarten, Auerhuhn und Haselhuhn, ermittelten wir Kombinationen komplementärer Habitatvariablen und zugehöriger Schwellenwerte, die gleichermaßen geeignete Lebensraumbedingungen bieten. Hierfür wurden Flächen mit und ohne Artvorkommen in drei Bergregionen der Schweiz verglichen und artrelevante Variablen, Variablenkombinationen sowie Schwellenwerte durch Generalisierte Lineare Gemischte Modelle und Conditional Inference Trees (CIT) identifiziert. Wichtige Lebensraummerkmale für beide Arten waren der Anteil der Heidelbeere (*Vaccinium myrtillus*) sowie die Anzahl tiefbeasteter Bäume und ein geringer Anteil Buche (*Fagus sylvatica*) in der Baumschicht. Das Vorkommen des Haselhuhns wurde zusätzlich durch die Anzahl an Ebereschen (*Sobus aucuparia*) und einen hohen Anteil an krautigen Pflanzen in der Bodenvegetation bestimmt, Randlinien zu offenen Flächen im Wald waren ein wichtiger, zusätzlicher Habitatfaktor für das Auerhuhn. Die ermittelten Schwellenwerte für Habitatvariablen waren meist nicht klar definiert, vielmehr galten unterschiedliche Werte abhängig davon, welche anderen, funktional ähnlichen Habitatmerkmale in einer Fläche vorhanden waren. Neben

der Identifikation artrelevanter Habitatvariablen kann die Bereitstellung alternativer Variablenkombinationen und kombinationsabhängiger Schwellenwerte eine wichtige Grundlage dafür liefern, Managementmaßnahmen flexibel an die in einem Waldbestand gegebenen Ausgangsbedingungen anzupassen.

Keywords: *Bonasa bonasia*, complementary habitat variables, Conditional Inference Tree, habitat management, mountain forests, *Tetrao urogallus*, thresholds

Introduction

In the human-dominated landscapes of Central Europe, where suitable wildlife habitat is limited, conservation management needs quantitative and spatially explicit prescriptions for biodiversity preservation and habitat restoration. In forest ecosystems, where species occurrence and diversity largely depends on characteristics of forest composition and structure (Bollmann et al., 2009; Brombacher, 1999), enhancing or restoring forest structural diversity is a prime goal of wildlife habitat management (Bergman et al., 2012; Lindenmayer & Luck, 2005). Yet, evidence-based, quantitative targets with regard to the amount, size and configuration of crucial habitat features (e.g. Müller & Bütler, 2010) are still rare. Moreover, even if quantitative management prescriptions exist, they are often not equally applicable to all site conditions: Most forests are commercially used ecosystems, characterized by a slow vegetation succession. Stand composition and structure differ greatly depending on site conditions and mode of exploitation (Bürgi, 1998), and thus provide variable conditions for habitat management. Possibilities for habitat management are further constrained by the objectives of commercial forestry, which may interfere with habitat management goals (Bollmann & Braunisch 2013). While some measures can readily be implemented, e.g. removing trees to create gaps, alter light conditions and promote ground vegetation, other structural components such as tree species composition or age structure can only be modified within long time frames, and in strict consideration of the initial state and local site conditions. Given these limitations, achieving the multiple functionalities of forests through integrative management remains a big challenge. This is particularly true when the requirements of different species with diverging ecological needs have to be met

87 within the same area. Yet, species rarely require similar habitat conditions
88 throughout their range, but avail themselves of a mosaic of different habitat
89 features and resources that offer complementary functionalities, such as food
90 supply, cover against predators, roosting or breeding sites. Thereby, different
91 habitat features may be interchangeable across a species' home range. Identifying
92 sets of important and complementary variables is thus a key for a flexible multi-
93 species habitat management.

94 In Europe, the hazel grouse *(Bonasa bonasia)* and the capercaillie *(Tetrao*
95 *urogallus)* are two forest grouse species of conservation concern (Storch, 2000)
96 which often occur sympatrically. Being considered as indicators for structural
97 diversity of boreal and mountain forest ecosystems (Pakkala et al., 2003; Suter et
98 al., 2002), they have suffered from habitat loss and degradation during the last
99 century mainly due to changes in forest management (Klaus, 1991). While
100 qualitative habitat requirements for these two tetraonids have been well described
101 (e.g. Glutz von Blotzheim et al., 1973; Müller, 1973), recent studies also provide
102 quantitative target values for particular habitat features, including variable
103 thresholds, which allow for targeted habitat management (Mathys et al., 2006;
104 Müller et al., 2009; Sachot et al., 2003; Schäublin & Bollmann, 2011; Suchant &
105 Braunisch, 2004). However, habitat recommendations vary considerably between
106 studies and areas, providing evidence for their limited generality.

107 In this study we analyse the habitat requirements of the two species from a novel
108 perspective: using multivariate classification and regression trees, we seek for
109 different combinations of habitat variables as well as quantitative thresholds
110 thereof that similarly promote species presence at the forest stand scale. In this
111 context we explore if and to what extent the required amount of one habitat

variable depends on the occurrence and amount of another, complementary habitat feature. Thereby we hypothesize that different threshold values apply for a given habitat feature which vary within the range of threshold-values found in literature. The quantitative prescriptions drawn for our analyses provide refined guidance for a flexible management and restoration of suitable forests for declining populations of the two tetraonids.

Materials and methods

Study area

The study was conducted in Switzerland, with the study sites distributed across three mountain ranges representing a broad gradient of bioclimatic conditions: the Jura Mountains (47°00’ N 6°40’ E - 47°30’ N 8°00’ E), Northern Prealps (46°30’ N 7°15’ E - 47°00’ N 9°30’ E) and Inner Alps (46°30’ N 9°00’ E - 47°00’ N 10°30’ E) (Fig. 1A). The Jura Mountains are characterized by a moderate climate with mild, dump summers and cold winters (MeteoSchweiz 2013, http://www.meteoschweiz.admin.ch). The mean annual ambient temperature is 5.5°C with 180 frost days and, on average, 2000 mm of rain and 4 m of snow annually at an altitude of 1200 m (MeteoSchweiz 2013). The tree line is around 1400 m a.s.l. (Steiger, 1994). The Northern Prealps are characterized by an Atlantic climate with high precipitation (2000-3000 mm/yr), cold-temperate winters and wet summers (MeteoSchweiz 2013). The tree line is at an elevation of approximately 2000 m (Steiger, 1994). The open and diversely structured forests are often adjacent to pastures and interspersed with mires. In the Inner Alps, the prevailing climate conditions are continental, with low precipitation (800-2000mm/yr), cold winters and warm and dry summers (MeteoSchweiz 2013).

Large, continuous forests belts are found along the valley slopes with the tree line being located at 2300m a.s.l. (Steiger, 1994). The altitudinal-climatic gradient is also reflected in the tree species composition, consisting of European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and Norway spruce (*Picea abies*) in the montane zone with larger proportions of larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) present in the most continental conditions of the subalpine zone.

Model species

The capercaillie is declining throughout its European distribution range (Storch 2007), being classified as "endangered" in Switzerland (Keller et al. 2010) where the number of displaying males was estimated between 450 and 500 in 2001 (half the size of the population in 1968/71; Mollet et al., 2003; Müller, 1973). Capercaillie prefers mature, open, coniferous or conifer-dominated mixed stands with an intermediate canopy cover (Bollmann et al., 2005; Suchant & Braunisch, 2004) and a rich ground vegetation cover, ideally including a high proportion of bilberry (Storch, 1993a). The species is considered to be an indicator for structural diversity in boreal and mountain forests, and plays the role of an umbrella species for some associated animal communities, as its presence is positively associated with the diversity and abundance of highly specialized mountain forest birds and forest-dwelling mammals (Pakkala et al., 2003; Suter et al., 2002). The hazel grouse is a territorial forest bird which requires semi-natural forests with young seral stages and old-growth stands with gaps (Desbrosses, 1997; cited in: Sachot, Perrin & Neet 2003). In the year 2001, 7500-9000 breeding pairs were estimated for Switzerland (Maumary et al., 2007). The hazel grouse is not threatened in

Europe (IUCN 2012, http://www.iucnredlist.org), however it is considered to be "near threatened" in Switzerland (Keller et al., 2010). Probably due to major differences in body size and mating system, home range and habitat preferences (in terms of forest structure and stand density) diverge between the two focal species. Distinct winter feeding habits also lead to discrepancies between the trophic niches, especially as regards resource trees. Local sympatric occurrence might arise from a patchy distribution of suitable hazel grouse habitat being embedded within a suitable capercaillie habitat matrix.

Species data

The presence data of the two focal species were drawn from the database of the Swiss Ornithological Institute (http://www.ornitho.ch) which compiles the data of the Swiss National Bird Monitoring programme. Direct (sightings) and indirect (feathers, faeces) species observations are collected year-round by a dense and area-wide network of species specialists and ornithologists, validated by experts of the Swiss Ornithological Institute, and allocated to the respective 1 km^2 cell of the Swiss National Grid. This cell size also corresponds to the size of a small capercaillie home range (100-1000 ha; Storch, 1995a) and to the double or triple of the home range of a hazel grouse (30-40 ha; Rhim & Lee, 2001). A pairwise sampling scheme was applied, selecting pairs of grid cells with species presence or absence (Table 1). Presence grid cells were chosen according to the following selection criteria: (1) there were at least three observations of the species within the years 2007 – 2010, (2) the sample contained different types of cells, namely cells with both single and sympatric occurrence of the two species, (3) the grid cells were distributed as evenly as possible within the respective study area and

along the altitudinal gradient (Fig. 1A). Absence grid cells with a forest cover of at least 50% were randomly selected within 1 km up to maximum 4 km distance to the corresponding presence cells to make sure that they could potentially be reached by the species. Although absence cells were only selected when there were no species records (indirect or direct) within the last 10 years, species presence could not be entirely ruled out, so that absence grid cells were in fact pseudo-absences. Yet, for reasons of simplicity they are referred to as "absence" here.

Habitat variables

Habitat variables were collected from June to August 2011 at 16 sampling plots of 30 x 30 m in size, regularly distributed within each grid cell (Fig. 1B,C, Table 1). The variables included information on stand structure, successional stage, tree species composition, ground vegetation and species-specific habitat features (Table 2). Depending on the spatial extent required to capture the respective structural attribute in sufficient detail, habitat variables were mapped at different reference areas within the sampling plot. Whereas variables describing stand structure and tree species composition in the canopy (≥ 5 m) and shrub layer (≥ 1.3 and < 5 m) were collected across the whole plot area, special resources like rowans (*Sorbus aucuparia*) and anthills were quantified within a 15 x 15 m nested square located around the plot centre (Fig. 1C), the two diagonal corners of which were used to assess the ground vegetation.

Statistics

Habitat selection

Habitat selection was analysed using Generalized Linear Mixed Models (GLMMs, R-package lme4; Bates et al., 2014) with a binomial error distribution (logit link) and "grid cell pair" as random factor. First, univariate models were run with all potentially relevant variables. From pairs of correlated explanatory variables (Spearman's $r_s \geq |0.7|$) the variable with the higher predictive performance in univariate models was retained. Multivariate models were then generated with the remaining set of significant variables, using a backward selection procedure until the model was reduced to twelve variables. Then, the "dredge" function (R-package MuMIn; Barton, 2012) was applied to identify the most parsimonious model from all possible combinations of the remaining variables according to Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). In case of non-significant differences between the top-ranked candidate models (ΔAIC of ≤ 2), model averaging was applied. The models were evaluated by assessing their discrimination ability using the area under the receiver operating characteristic (ROC) curve (AUC) (R-package pROC, Robin et al., 2011) as well as their calibration, i.e. the extent to which the observed proportion of species presence equates to the model's estimated presence probabilities (sensu Jiménez-Valverde et al., 2013).

Variable thresholds

Conditional Inference Trees (CIT) were used for the identification of variable thresholds explaining species presence. This method, similar to classification and regression trees, uses recursive partitioning to select significant predictor variables in a hierarchical way and to identify the best cut-off values that split the dataset so as to predict species presence and absence (Hothorn et al., 2006). It is therefore a

valuable tool for deriving quantitative variable thresholds for habitat management (Müller & Bütler, 2010). The model starts with univariately testing for independence between the response and each of the predictor variables. If this hypothesis cannot be rejected, the calculation stops - otherwise the split for the variable with the strongest association is applied. The procedure is recursively repeated with each of the remaining subsets until no significant split is found. A Bonferroni correction was used to account for multiple testing.

Variable thresholds were first calculated univariately for all variables that had been identified as being significant in the GLMMs. The 95% confidence interval of each threshold value was quantified by bootstrapping and the obtained value-ranges compared to the threshold values provided by other studies.

Multivariate CIT were then generated to identify variable combinations and threshold thereof that provide suitable structural conditions at the plot-level so as to guide the management of forest stands. Based on the results, we also calculated the percentage of suitable plots per grid cell (i.e. plots with a predicted probability of species' presence > 0.5) to obtain information about the required proportion of suitable habitat in the stand mosaic. Conditional Inference Trees were calculated with the R-package party (Hothorn et al., 2011) setting the minimum sum of weights for splitting (minsplit-criterion) to 100. The models' predictive performance and consistency were evaluated by calculating AUC (package pROC, (Robin et al., 2011)) and calibration. All statistical analyses were done with the Software R (R Development Core Team 2011).

Results

Habitat selection

The important habitat variables identified for both grouse species resembled those of former studies: The probability of capercaillie occurrence was best explained by the following variables: The number of basal-branched trees, the cover of ground vegetation, particularly of bilberry, as well as the presence of inner forest edges positively influenced the occurrence probability of capercaillie, while the proportion of fir and beech in the canopy layer was negatively related to species presence (Table 3). The presence probability of hazel grouse was positively affected by the number of basal-branched trees, the number of rowans (*Sorbus sp.*), the bilberry cover and the proportion of herbs and ferns in the ground vegetation. A high proportion of beech and deciduous trees other than feeding trees (s. Table 2) in the canopy layer, as well as outer forest edges negatively affected the presence probability (Table 4). With an AUC of 0.85 and 0.86 for capercaillie and hazel grouse, respectively, and a consistent calibration (Fig. 2) both models performed very well in predicting species presence (Hosmer & Lemeshow, 2000).

Variable thresholds

The two target species showed a similar selection pattern for several crucial habitat variables. Confidence intervals largely overlapped between species and mostly encompassed the species-specific threshold values provided by other studies (Table 5):

The canopy cover threshold for capercaillie indicated an upper limit at 81% (95% confidence interval [CI] of the threshold: 60 – 83%) which was rather high compared to the values of 25 – 70% obtained in other studies (Bollmann et al., 2008; Bollmann et al., 2005; Lieser & Roth, 2001; Storch, 1993a). For hazel

grouse this threshold was lower with 60% (CI: 60 – 81%), but still exceeded the results of Mathys (2000)(40 – 50%).

The canopy layer on sites with capercaillie presence was composed of spruce by at least 5 % (CI: 1 - 11%) which corresponded roughly to the lower limit of 10 – 33% indicated by Suchant and Braunisch (2004). For hazel grouse, a minimum value of 10% (CI: 5-16%) was found. Furthermore, there was an upper limit for deciduous trees other than beech for both species, at 19% (CI: 12-28%) for capercaillie and 14% (CI: 0 – 18%) for hazel grouse. While these trees are rarely used as food resource and provide neither sight nor thermal protection in winter, the beech buds represent an important food resource in late winter and spring. Nevertheless, in our model both grouse species showed only little tolerance towards beech in the canopy (upper threshold of 3%) although the confidence intervals suggest that higher amounts of beech in the canopy layer are accepted.

Both grouse species required a minimum of 60% of ground vegetation cover (CI: 28 – 60% for capercaillie; 38-60% for hazel grouse) which corresponded to literature specifications (Bollmann et al., 2008; Bollmann et al., 2005; Lieser & Roth, 2001; Storch, 1993a). For the hazel grouse, herbs covering the ground ideally exceeded 18 % (CI: 13 – 38 %); slightly higher values but with a greater variance were obtained for capercaillie (38 %, CI: 0 -62%). Very low threshold values were obtained for important food resources like bilberry cover and the proportion of resource trees in the shrub and the canopy layer (1% for both species and variables). Moreover, a minimum of one rowan (≥ 3 m tall) and of one basal-branched tree was required per plot (900 m^2), the former being a little lower than what Schäublin and Bollmann (2011) found for hazel grouse (2 rowans/900

311 m^2). While outer forest edges were avoided, both species showed a preference for
312 inner forest edges which is in accordance with Bollmann (2006).

313

314 Complementary variable combinations

315 The multivariate CIT for capercaillie (Fig. 3A) and hazel grouse (Fig. 3B) showed
316 that suitable habitat (defined here as sites with a probability of species presence
317 $p \geq 0.5$) can be obtained by different variable combinations.

318 The multivariate tree for capercaillie provided four possible combinations of
319 explanatory variables that resulted in a probability of species occurrence greater
320 than 50% (see Fig. 3A). If, in a given plot, bilberry is available, the ground
321 vegetation cover exceeds 53%, and at least one basal-branched tree per $900m^2$ is
322 present, the probability that capercaillie occurs is 83% (option 1). In the absence
323 of basal-branched trees this probability decreases to 68% (option 2), and with a
324 ground vegetation cover of less than 53%, the presence probability is further
325 reduced to 50% (option 3). With no bilberry present, at least three basal-branched
326 trees have to be available to obtain a 61% probability of capercaillie presence. The
327 model showed a good ability to correctly discriminate between species presence
328 and absence (AUC = 0.75).

329 To obtain a probability of hazel grouse presence of at least 50%, again four
330 possible variable combinations could be prescribed according to the multivariate
331 CIT (see Fig. 3B): if bilberry cover is present, and at least one basal-branched tree
332 is present, the probability of hazel grouse occurrence is 83% (option 1); without
333 such a tree but with bilberry cover of more than 31% there is still a 79%
334 probability that the hazel grouse occurs under such habitat conditions (option 2).
335 In sites with a lower or no bilberry cover a probability of presence of 57% will

still be reached (options 3 and 4). With an AUC of 0.76, this CIT showed good discrimination ability

The probability of capercaillie occurrence was over 70% in grid cells of 1 km^2 with sampling plots having of suitable habitat in more than 63% (CI: 0.33 - 0.91) (Fig. 4A). More than 75 % (CI: 0.25 - 0.90) of the plots within a grid cell had to be suitable for hazel grouse in order to increase its probability of presence from 30% to almost 80% (Fig. 4B).

Discussion

Similar habitat associations of the two species

Even if this study overall corroborates previous findings about habitat selection of capercaillie and hazel grouse, it indicates less contrasting habitat associations than previously established. The novelty of our research lies in the finding of combinations of habitat variables that all provide acceptable if not suitable habitat conditions for both grouse species. This increases the flexibility of managers in developing area-specific solutions for species conservation.

A previously established major difference in the ecological association of the two grouse species is a preference for different seral stages. While hazel grouse is considered to prefer younger forests (Klaus, 1991; Mathys et al., 2006), capercaillie is generally associated with old growths (Rolstad & Wegge, 1987). We could not find a clear cut preference for any given successional stage, neither for hazel grouse nor for capercaillie. This might be due to the fact that our study sites mainly consisted of multi-aged stands without extended old growths. The variable with the strongest association with capercaillie presence was bilberry cover. Another important variable was ground vegetation cover, which decreases

as the canopy becomes denser. A well-developed field layer provides shelter against predators to chick-rearing hens and food supply in the form of buds and berries (e.g. *Vaccinium myrtillus*, Lakka & Kouki, 2009). When the field layer was limited, basal-branched trees took over as shelter and vice versa. According to Bollmann et al. (2005) and Lanz and Bollmann (2008), basal-branched Norway spruce *Picea abies* typically represent the favourite resting trees for capercaillie, especially when these trees are situated in forest stands with two or more aisles as this eases soaring and landing (Lanz & Bollmann, 2008). Therefore it is also not surprising that capercaillie preferred the presence of inner forest edges. There is a trade-off, however, between woodland openness and closure due to an increased predation risk when the habitat is too open, as demonstrated for other grouse species (Signorell et al., 2010). Especially the hazel grouse avoided outer forest edges. Edge effects typically caused by increased habitat fragmentation have been shown to augment the risk of egg-predation in grouse that nest on the ground (Storch, 1995b). Moreover, the hazel grouse is the poorest disperser among grouse species, which renders it very vulnerable to patch isolation (Åberg et al., 1995; Sahlsten, 2007): gaps larger than 150 - 250 m in diameter already represent a serious obstacle to dispersal (Åberg et al., 1995; Montadert & Léonard, 2006; Sahlsten, 2007). While both species' avoidance of beech-dominated stands was not surprising, capercaillie presence was also negatively related to the proportion of white fir *(Abies alba)*. This is in contrast with previous studies demonstrating a preference for this tree species, particularly as food resource in winter (e.g., Lanz & Bollmann, 2008), although preferences for particular conifer species (Storch, 1993b) have been found to vary greatly between regions (Lanz & Bollmann, 2008; Lieser, 1996; Siano, 2011; Storch, 1993b). Across our study area the abundance of white fir was overall low and frequently associated with beech-

dominated stands in the lower altitudes otherwise representing structurally suboptimal habitat conditions, which may explain this result. Hazel grouse has been shown to prefer mixed or coniferous stands over pure deciduous stands (Klaus, 1991; Montadert & Léonard, 2006), which is corroborated in this study. Although several deciduous trees act as important resource trees, coniferous trees in the shrub layer remain essential as they provide better sight protection from predators and enhanced thermal benefits, especially in winter (Swenson et al., 1995; Swenson & Olsson, 1991). Yet, despite explaining species presence very well, our variable set may not fully represent the two species' requirements, since large-scale habitat characteristics such as stand mosaic heterogeneity, forest gaps and linear structural elements cannot be sufficiently captured by a plot-based sampling design. Area-wide structural variables obtained from remote sensing, such as Airborne Laser Scanning, aerial or satellite images have been shown add valuable complementary information which can substantially improve the predictive performance of habitat models (Zellweger et al., 2014) and - in our case - may have revealed greater species-specific differences in habitat selection.

Variable thresholds

While the threshold-ranges obtained for most variables encompassed the values found in literature, for some relevant habitat variables our thresholds were strikingly lower. This concerns for instance the proportion of bilberry in the field layer, a feature relevant for both species. Former studies indicated 15 – 70% bilberry cover for capercaillie and 40% for hazel grouse (Baines et al., 2004; Schäublin & Bollmann, 2011), which contrasts with our > 0% for capercaillie and >1% for hazel grouse. Regional variation in both food supply and diet (i.e. the

availability and use of other, complementary food resources), can explain this divergence. For example, in the dry Eastern part of the study area the abundance of bilberry is generally low and replaced by other food items (Bollmann et al. 2005). Still, methodological issues cannot entirely be ruled out: Small patches with locally high proportions of *Vaccinium myrtillus* may be sufficient within an individual's home range, but may have been missed by our plot-based sampling. Differences in variable thresholds may further result from different statistical methods (Manel et al., 2001), sampling resolutions, study regions as well as varying seasons (Table 5). Moreover, most of the studies were conducted within small study regions with limited representativeness (Braunisch & Suchant, 2010; Graf et al., 2006).

The effects of grain and extent upon the generality of habitat selection analyses have been subject to several studies (Braunisch & Suchant, 2010; Graf et al., 2006; Thuiller et al., 2004). It is widely acknowledged that increasing the spatial extent of the study area generally increases the representativeness of the results because one then encompasses a greater proportion of a species' distribution and environmental gradient. In practice, however, the unavoidable trade-off between sampling resolution and extent persists, mostly due to time constraints and limited manpower. Braunisch and Suchant (2010) showed that coarse-grained data, sampled over a wide representative area, outperform very precise data systematically collected from a restricted, less representative region. As our data was collected over three Swiss mountain ranges at a 1 km^2 resolution, we are confident about the generality of our results despite its fairly coarse resolution. In addition, particularly in highly mobile species, a coarse sampling resolution matching the species-specific home ranges, can even be advantageous for

appraising habitat selection, as the required habitat mosaic is also be taken into account (Braunisch & Suchant, 2010).

Threshold ranges

Some of the habitat variable thresholds have broad confidence intervals. One may argue that this is merely due to the variation between plots within the 1 km^2 grid cells, and that narrower confidence intervals would have been obtained if variables would have been mapped at a higher resolution (e.g. just around bird sighting location). Actually, we tested for such an effect, mapping the habitat at a 25 x 25 m resolution within a subregion of 1772 ha (Forest Reserve Amden, Northern Prealps, 1040 m a.s.l., 47°10'N 9°13'E): similar thresholds with equally broad confidence intervals were obtained (Appendix A). Therefore, our large confidence intervals indicate that there is not one clear-cut quantitative threshold, but rather a "threshold zone" (Huggett, 2005) that may serve for habitat management. The multivariate CIT finally show how, depending on the local conditions (i.e. differences in presence and abundance of other variables), a single variable can exhibit different threshold values, all falling within the confidence intervals obtained from univariate CIT. A good example is provided by the multivariate tree for capercaillie occurrence (Fig. 3A). Here, the variable "number of basal-branched trees" has two thresholds: with a higher ground vegetation cover, a lower number of such trees is required, and vice versa. Both thresholds typically contribute to a capercaillie presence probability greater than 50% under different conditions, which delivers flexible guidance for habitat management.

Combined habitat variable sets

462 Multivariate CITs enable visualizing, under the form of a classification tree, the
463 information about the importance and interaction of different variables. It
464 therefore provides a promising user-friendly tool that can deliver pragmatic,
465 flexible quantitative management criteria to practitioners by presenting different
466 pathways for receiving a favoured goal (e.g. a probability of species presence of at
467 least 50%). The probability of species presence resulting from a specific
468 combination of habitat variables is graphically depicted by branches of the tree,
469 which facilitates interpretation (Fig. 3).

470 Yet, one drawback of conditional inference trees is that one cannot account for
471 data clustering, e.g. by including spatial random factors in the models. Although
472 our species data were recorded for 1 km^2 grid cells, we applied the CIT to the
473 plot-data to capture the full variety of different variable combinations within an
474 individuals' home range, without smoothing out the heterogeneity between
475 sampling plots, e.g. by averaging the variable values across the grid cell.
476 Averaging all the plot values per grid cell and calculating the thresholds from the
477 averaged values may have biased the results towards intermediate values. Hence,
478 important information about species' preferences, for instance under more
479 marginal circumstances, would have been lost. This was possible as the variance
480 between the plots of the same grid cell did not differ from those between
481 randomly chosen plots of different grid cells of the same category
482 (presence/absence). Moreover, our grid cells do not correspond to the presence of
483 a single individual but rather an area where the species occurs. The area is hosting
484 at least one but most likely several individuals, with the plots in a grid cell thus
485 representing the gradient of species-specific environmental conditions. Our dual
486 approach, using a GLMM to pre-select the important habitat variables that were
487 entered in the CIT, nevertheless accounts for spatial clustering in the first analysis

step, which makes us confident that the plot-based results provide a useful approximation of the variable thresholds at the forest stand level.

Conclusions

Our approach generates complementary, interchangeable habitat variable sets and variable thresholds at both the forest stand (conditions per plot) and the forest mosaic (proportion of suitable habitat per grid cell) scale that all deliver suitable conditions for our model species. With that we provide applicable quantitative prescriptions for habitat management that allow practitioners to take the local conditions into accountand to find a good solution for integrating timber production and biodiversity preservation and restoration in multi-functional forests. Our findings revealed that the two model species have less contrasting habitat requirements as expected. This could be an indicator of their behavioural and ecological congruence which may allow them to exploit similar habitats and greatly simplifies management in areas of sympatric occurrence. Accompanied by analyses of landscape suitability at the meta-population level, which allow priority areas to be delineated (Bollmann et al., 2011; Braunisch & Suchant, 2007; Graf et al., 2005), the approach used here advances the development of multiple-species conservation strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Tables

Table 1. The number of presence and absence grid cells (1 km^2) per species, as well as the number of embedded sampling plots (30 x 30 m) (in parentheses) used for the analysis.

	Presence	**Absence**
Capercaillie	50 (609)	50 (526)
Hazel Grouse	72 (771)	71 (627)

710 Table 2. List of habitat variables with the reference area (R.area) at which they
711 were collected: P = Plot (30 x 30 m), NS = Nested square (15 x 15 m), GV =
712 Nested square quarters (7.5 x 7.5 m) for ground vegetation (see Fig. 1C). DBH:
713 stem diameter at breast height, p/a: presence/absence.

Category	Variable Code	Description	Unit	R.area
Successional stage	SUCC_STAGE	Age of the forest stands subdivided into 5 age-classes: 1 = regeneration (<1.3m height) 2 = thicket (<10cm DBH) 3 = pole stage (<30cm DBH) 4 = tree stage (<60cm DBH) 5 = „old“ forest (≥ 3tr. ≥60cm DBH) 6 = multi-age stands	categorical (1-6)	P
Stand structure	STAND_STRU	Vertical structure as number of layers, 1 = one, 2 = two 3 = multi layered	categorical (1-3)	P
Ground vegetation distribution	GV_DIS	Pattern of ground vegetation: 1=homogeneous, 2=patchy, 3=clumped	categorical (1-3)	P
Vegetation cover	CAN_COV	Canopy (≥5m) cover	%	P
	SHRUB_COV	Shrub (≥1.3m, <5m) cover	%	P
	GV_COV	Ground vegetation (<1.3m) cover	%	GV
Canopy composition	CAN_BEE	Percentage of beech *(Fagus sylvatica)*	%	P
	CAN_O_DEC	Percentage of deciduous trees (excluding beech and resource trees)	%	P
	CAN_FIR	Percentage of fir (*Abies alba)*	%	P
	CAN_LAR	Percentage of larch (*Larix decidua*)	%	P
	CAN_RES_TR	Percentage of resource trees *(Sorbus* sp., *Salix* sp., *Betula* sp., *Alnus* sp., *Corylus* sp. and *Sambucus* sp.)	%	P
	CAN_SPR	Percentage of spruce (*Picea abies*)	%	P
	CAN_PIN	Percentage of pine (*Pinus* sp.)	%	P
Shrub composition	SHR_BEE	Percentage of beech	%	P
	SHR_O_DEC	Percentage of deciduous trees (excluding beech and resource trees)	%	P
	SHR_FIR	Percentage of fir	%	P
	SHR_LAR	Percentage of larch	%	P
	SHR_RES_TR	Percentage of resource trees	%	P
	SHR_SPR	Percentage of spruce	%	P
	SHR_PIN	Percentage of pine	%	P
Ground vegetation	GV_HEI	Ground vegetation height	cm	GV
	COV_CON	Cover of coniferous regeneration	%	GV
	COV_DEC	Cover of deciduous regeneration	%	GV
	COV_HERB	Cover of herbs	%	GV
	COV_FERN	Cover of ferns	%	GV
	COV_GRAS	Cover of grasses	%	GV
	COV_BER	Cover of berry plants	%	GV
	COV_VAC	Cover of bilberry *(Vaccinium myrtillus)*	%	GV
Special Ressources	ROW_TOT	Number of Rowans ≥3m *(Sorbus aucuparia)*	n	NS
	ANT_HILL	Number of ant hills	n	NS

	Functional trees	BB_TREE	Basal-branched trees	n	P
	Ecotones	E1	Presence/absence of inner forest edge	p/a	P
		E2	Presence/absence of outer forest edge	p/a	P

714

715

Table 3. Habitat variables explaining the presence of capercaillie, obtained from a Generalized Linear Mixed Model (GLMM) with "grid cell-pair" as random factor. Variable estimates, as obtained from averaging the four best models according to the AIC-ranking, are presented and the relative variable importance is provided in parentheses. The composition and ranking of the included models is specified in the lower part of the table. Asterisks indicate significance levels with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = non-significant. Variable codes are explained in Table 2.

No.	**Variables (fixed effects)**	**Estimate**	**SE**	**Sign.**
1	BB_TREE (1)	0.158	0.041	***
2	CAN_BEE (1)	-0.029	0.009	***
3	CAN_FIR (1)	-0.030	0.012	*
4	COV_HERB (0.81)	0.011	0.006	n.s.
5	COV_VAC (1)	0.045	0.008	***
6	E1 (1)	0.760	0.347	*
7	E2 (0.81)	-0.613	0.326	n.s.
8	GV_COV (1)	0.012	0.005	*
9	ROW_TOT (0.78)	0.056	0.033	n.s.
Grouping factor (random effect)		**Variance**	**CI**	
1	Pair_ID (Intercept)	1.933	1.339-3.032	
Rank	**Incl. Variables (No.)**	**AICc**	**ΔAICc**	**ΔAICc weight**
1	1/2/3/4/5/6/7/8/9	941.59	0	0.39
2	1/2/3/4/5/6/7/8	942.73	1.14	0.22
3	1/2/3/5/6/7/8/9	943	1.41	0.19
4	1/2/3/4/5/6/8/9	943.05	1.46	0.19

Table 4. Habitat variables explaining the presence of hazel grouse, obtained from a Generalized Linear Mixed Model (GLMM) with "grid cell-pair" as random factor. Variable estimates, as obtained from averaging the four best models according to the AIC-ranking, are presented and the relative variable importance is provided in parentheses. The composition and ranking of the included models is specified in the lower part of the table. Asterisks indicate significance levels with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = non-significant. Variable codes are explained in Table 2.

	Variable	**Estimate**	**SE**	**Sign.**
1	BB_TREE (1)	0.268	0.047	***
2	CAN_BEE (1)	-0.023	0.006	***
3	CAN_O_DEC (1)	-0.032	0.012	**
4	COV_DEC (1)	-0.031	0.011	**
5	COV_FERN (1)	0.023	0.009	*
6	COV_HERB (1)	0.022	0.005	***
7	COV_VAC (1)	0.044	0.006	***
8	E2 (1)	-0.911	0.271	***
9	ROW_TOT (1)	0.099	0.035	**
10	SHR_O_DEC (1)	-0.053	0.019	**
11	SHR_RES_TR (0.68)	0.022	0.012	n.s.
Grouping factor (random effect)		**Variance**	**CI**	
	Pair_ID	1.554	1.398-2.243	
Rank	**Incl. Variables (No.)**	**AICc**	**ΔAICc**	**ΔAICc weight**
1	1/2/3/4/5/6/7/8/9/10/11	1267.78	0	0.68
2	1/2/3/4/5/6/7/8/9/10	1269.28	1.5	0.32

734 Table 5. Thresholds for the variables significantly explaining the occurrence of
735 each of the two model species (see Table 3 and 4), calculated using univariate
736 Conditional Inference Trees (CIT) and compared to thresholds (indicated by </>)
737 and optimal variable ranges found in literature. n.s. = no significant split.

Explanatory variable	**Thresholds**		**Literature**[1,2]	
	Capercaillie	Hazel grouse	Capercaillie	Hazel grouse
n(presence/absence)	n(800/593)	n(477/667)		
CAN_COV (%)	≤81 (60-83)	≤60 (60-81)	25-65 [1] 40-60 [2] 50 [3] <60 [5] 50-70 [6]	40-50 [4]
CAN_SPR (%)	>5 (1-11)	>10 (5-16)	10-33 [6]	
CAN_FIR (%)	≤24 (3-33)	≤10 (1-33)		
CAN_BEE (%)	≤3 (2-26)	≤3(0-11)		
CAN_O_DEC (%)	≤19 (12-28)	≤14 (0-28)		
CAN_RES_TR (%)	>1(0-2)	>1 (0-5)		
SHRUB_COV (%)	n.s.	≤26 (15-40)		
SHR_RES_TR (%)	n.s.	>0 (0-2)		>10 [5]
SHR_O_DEC (%)	n.s.	≤6 (3-18)		
GV_COV (%)	>60 (28-60)	>60 (38-60)	>40 [6] 50-70 [7] >60 [5] [1] >70 [2] 90-100 [3]	30-45 [5] 60-100 [4]
COV_VAC (%)	>0 (0-3)	> 1 (0-1)	15-20 or more [8] >20 [5] ≥60 [10] >70-100 [7]	40 (+-4) [11]
COV_HERB (%)	>38 (0-62)	>18 (13-38)		
COV_GRAS (%)	n.s.	>3 (1-17)		
COV_DEC (%)	n.s.	≤13 (8-25)		
ROW_TOT (no./900m^2)	>0 (0-2)	>0 (0-1)		2/900m^2 [11]
BB_TREE (no./900m^2)	>0 (0-1)	>0 (0-5)		
E1 (0;1)	=1	=1	The more the better [9]	
E2 (0;1)	=0	=0		

[1]**References:** [1] Bollmann et al. 2005, [2] Bollmann et al. 2008, [3] Storch, I. 1993, [4] Mathys et al. 2006, [5] Lieser and Roth 2001, [6] Suchant and Braunisch 2004, [7] Ehrbahr et al. 2011, [8] Baines et al. 2004, [9] Bollmann, K. 2006, [10] Müller, F. 1973, [11] Schäublin & Bollmann 2011

[2]**Season and spatial scale of the studies:** [1] spring, 25x25m plots; [2] winter&summer 25x25m; [3] plot with r=10m; [4] autumn, 0.8ha; [5] forest stand scale; [6] summer & winter, forest stand scale (1-50ha); [7] forest stand scale; [8] forest stand scale; [9] summer, Scotland, 64m^2; [10] area not specified; [11] winter, 25x25m

738 **Figure captions**

739 Fig. 1. Sampling design. Distribution of presence grid cells (black: capercaillie
740 presence, white: hazel grouse presence and dark grey: sympatric occurrence)
741 within three biogeographic mountain regions (highlighted in grey) of Switzerland:
742 Jura mountains (JM), Northern Prealps (NPA) and Inner Alps (IA) (A). For each
743 presence grid cell, an absence grid cell (not depicted on this map) was selected
744 within 1 - 4 km distance. In each grid cell, habitat variables were collected in
745 every sampling plot which was located in the forest (maximum 16 per grid cell)
746 (B). In a sampling plot, variables were collected at different reference areas (C):
747 within the entire 30 x 30 m plot, within a nested square (15 x 15 m) (white) or
748 within the two diagonal quarters of the nested square (7.5 x 7.5 m). The variables,
749 their unit and corresponding reference area for sampling are listed in Table 2.
750
751 Fig. 2. Model evaluation: Calibration plot showing the modelled probabilities of
752 species presence (*x*-axis) against the observed proportion of presence points (*y*-
753 axis) for 10 equal-sized probability intervals. Open symbols: capercaillie, filled
754 symbols: hazel grouse, squares: Generalized linear mixed models (GLMM),
755 triangles: conditional inference trees (CIT), solid line: perfect calibration. As a
756 classification method, CIT returns probability classes instead of continuous
757 probability values. Consequently, the bins with values correspond to the
758 probability classes shown in Figs 3A and B. In addition, the AUC-values of the
759 corresponding models are indicated.
760
761 Fig. 3. Multivariate Conditional Inference Trees (CIT) (minsplit=100) explaining
762 the presence of (A) capercaillie and (B) hazel grouse. The columns at the end of
763 each branch illustrate the probabilities of species presence (values from 0 to 1 are

given on the right side of each bar) resulting from a specific variable combination. Abbreviations of the habitat variables are explained in Table 2.

Fig. 4. CIT (minsplit = 10) depicting the thresholds for the proportion of suitable habitat (i.e. proportion of plots with a probability of presence ≥ 0.5) per grid cell explaining the presence of (A) capercaillie and (B) hazel grouse, respectively. Presence probabilities (dark grey) are given in values from 0 to 1. The 95% confidence intervals (CI) of the threshold values based on 1000 bootstrap replicates are as follows: (A) CI: 0.33- 0.91 and (B) CI: 0.25 - 0.90).

Figure 1
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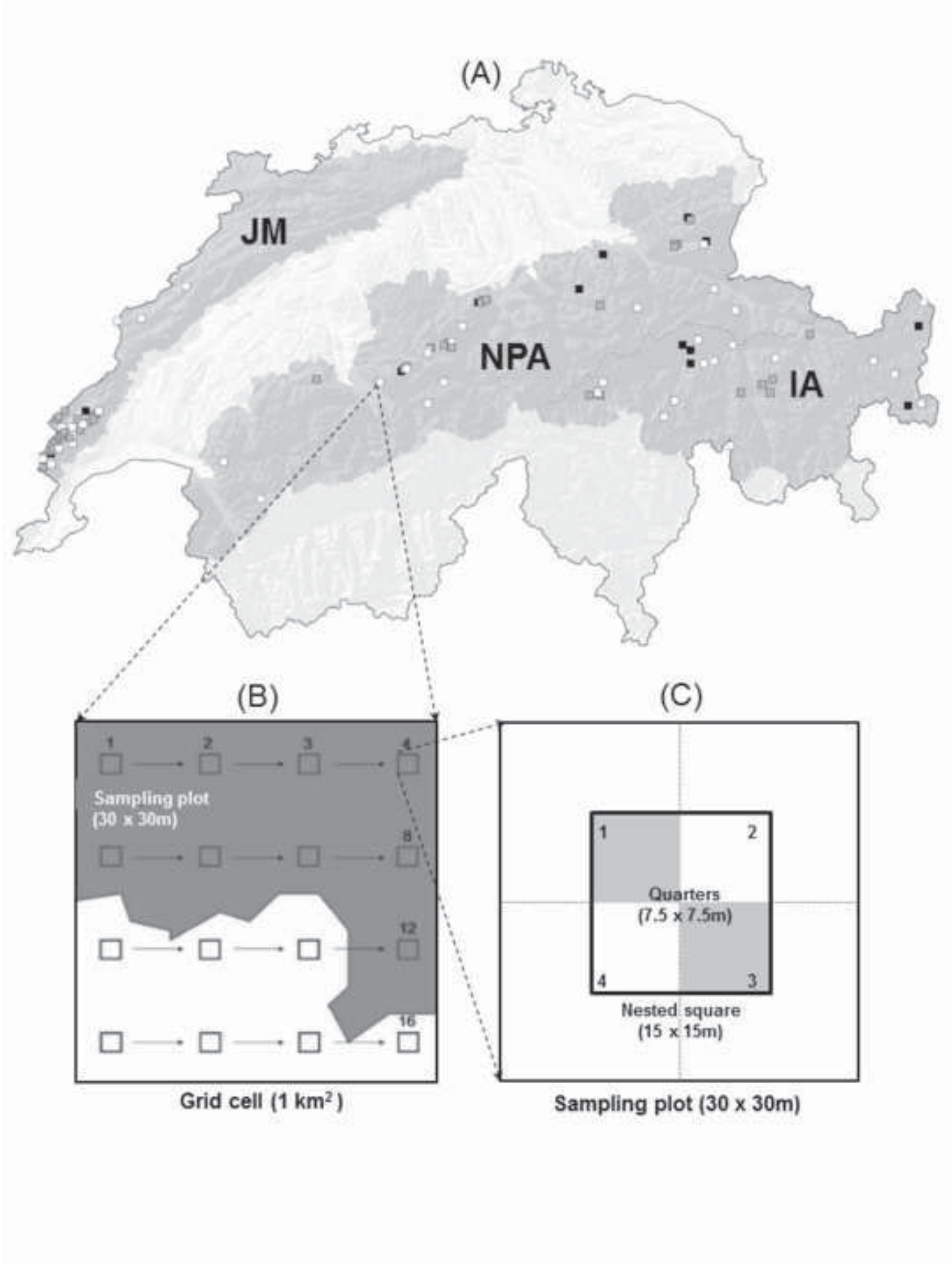

Figure 2
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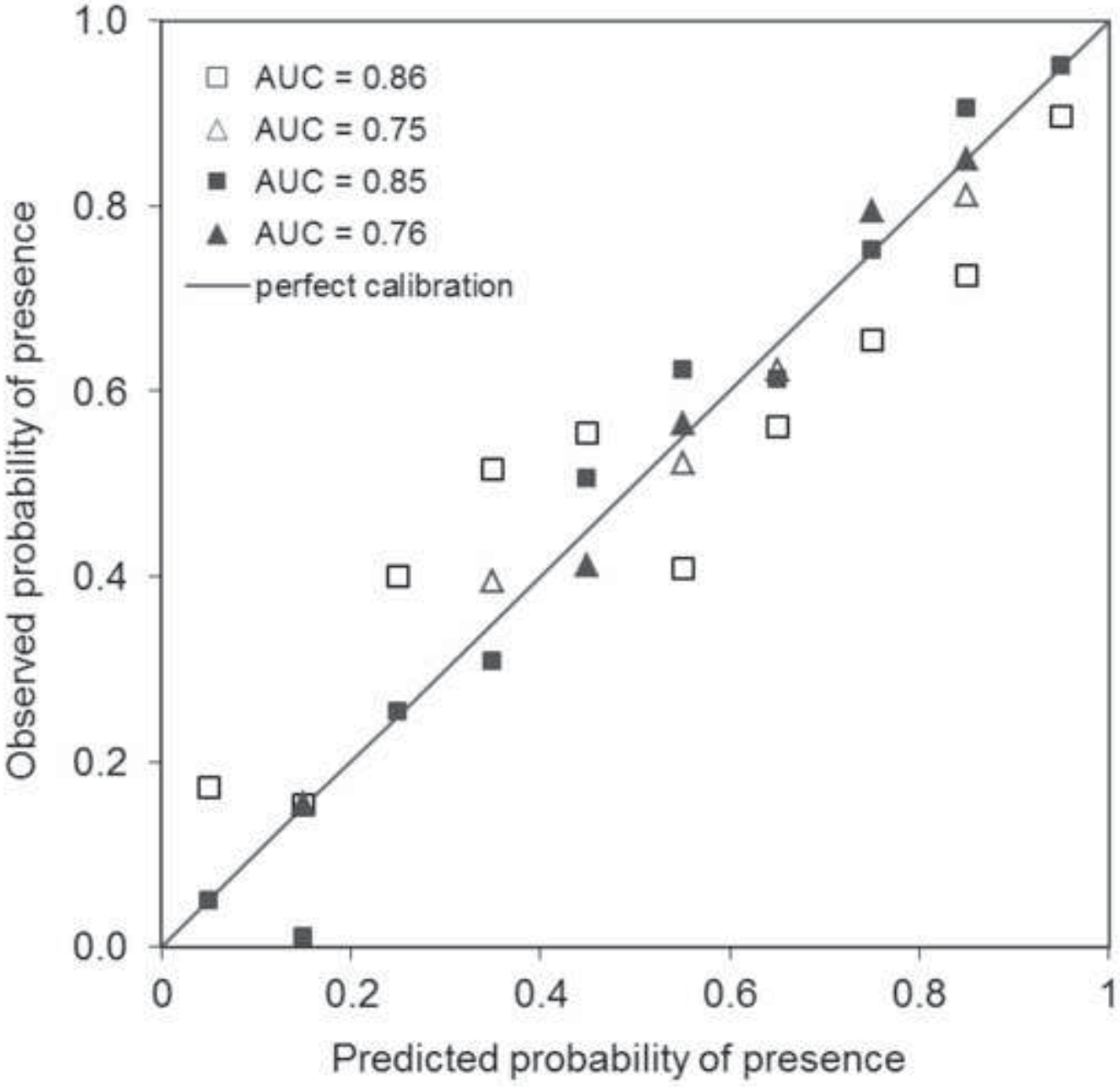

Figure 3A

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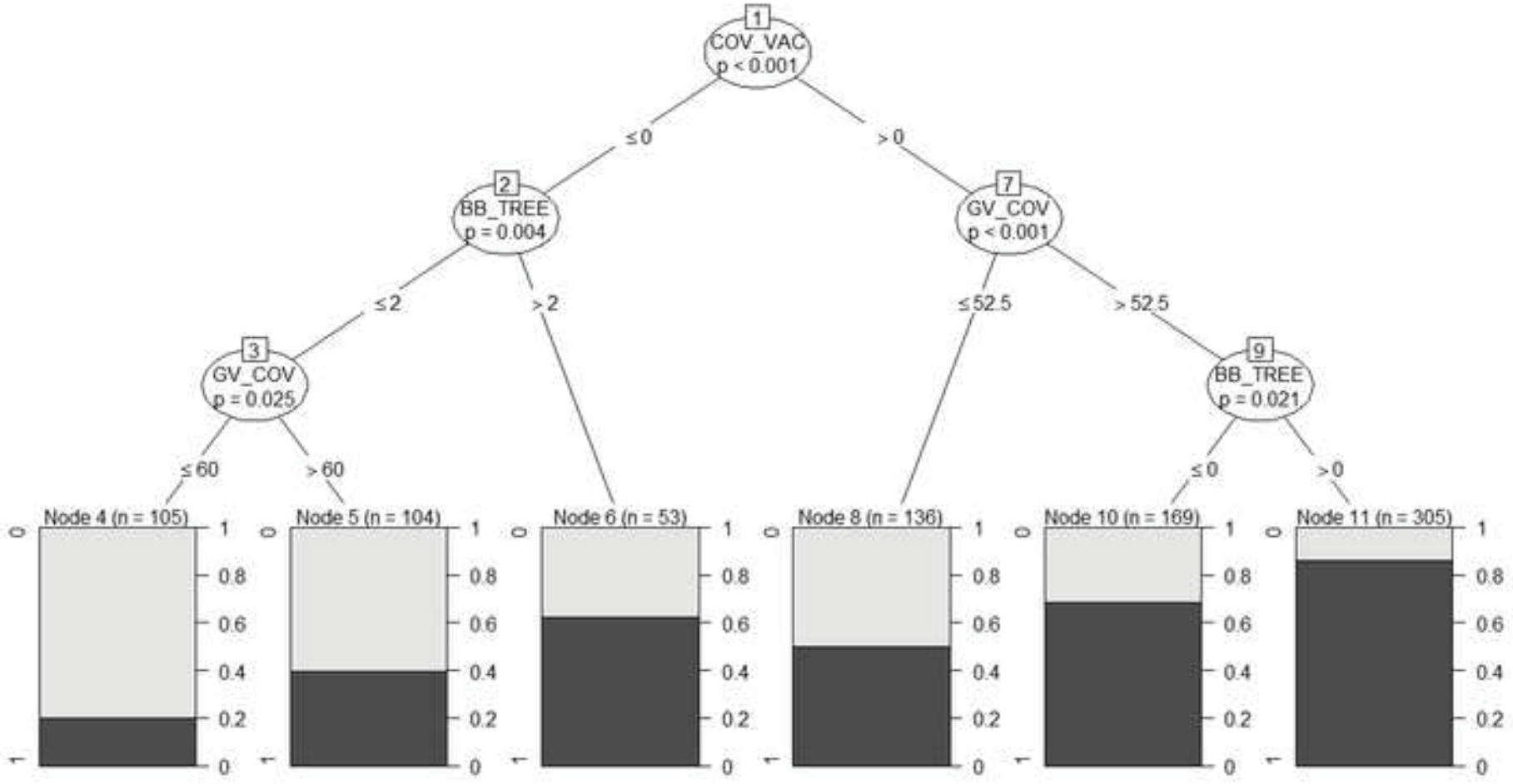

Figure 3B

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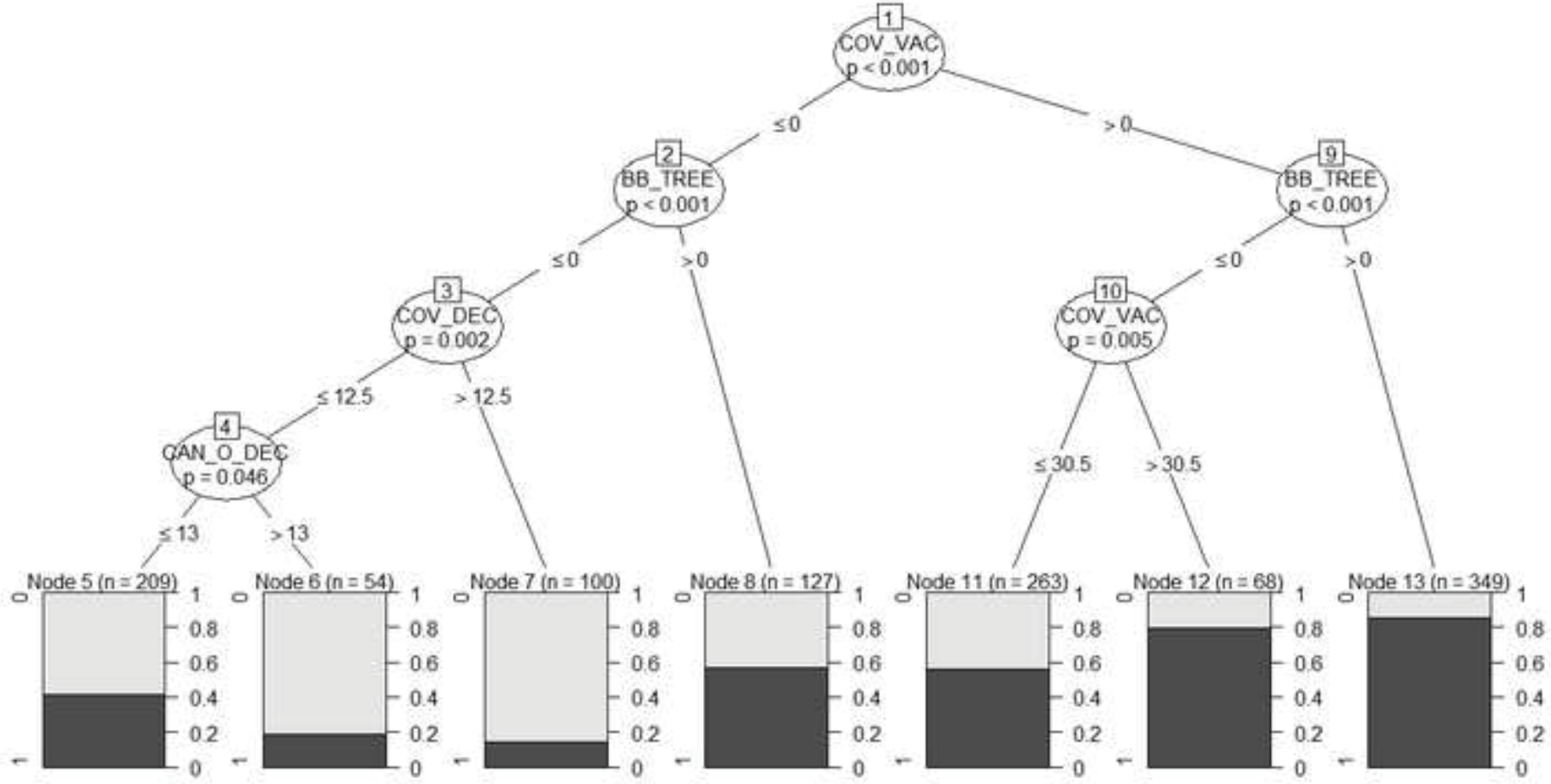

Figure 4A

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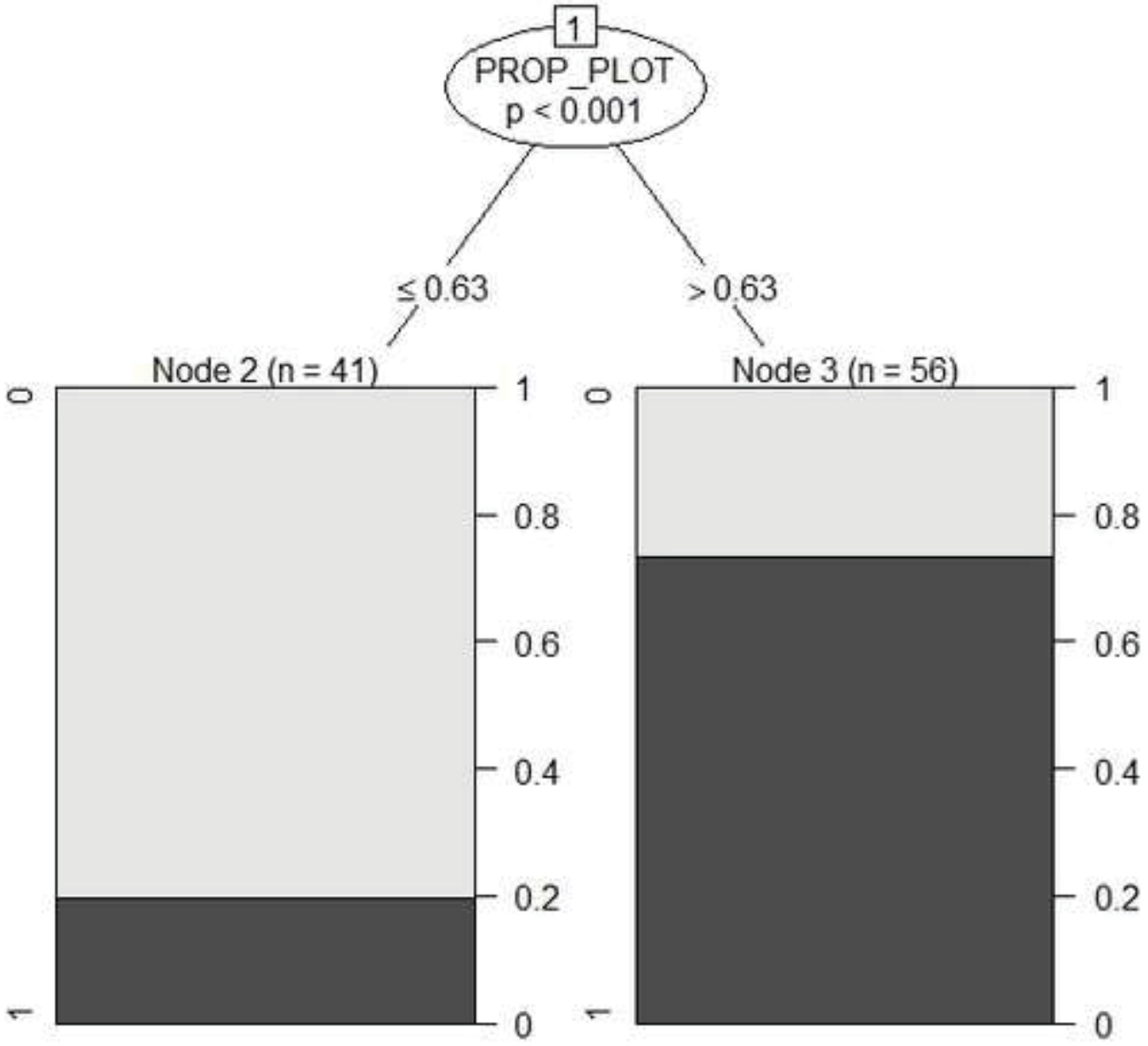

Figure 4B

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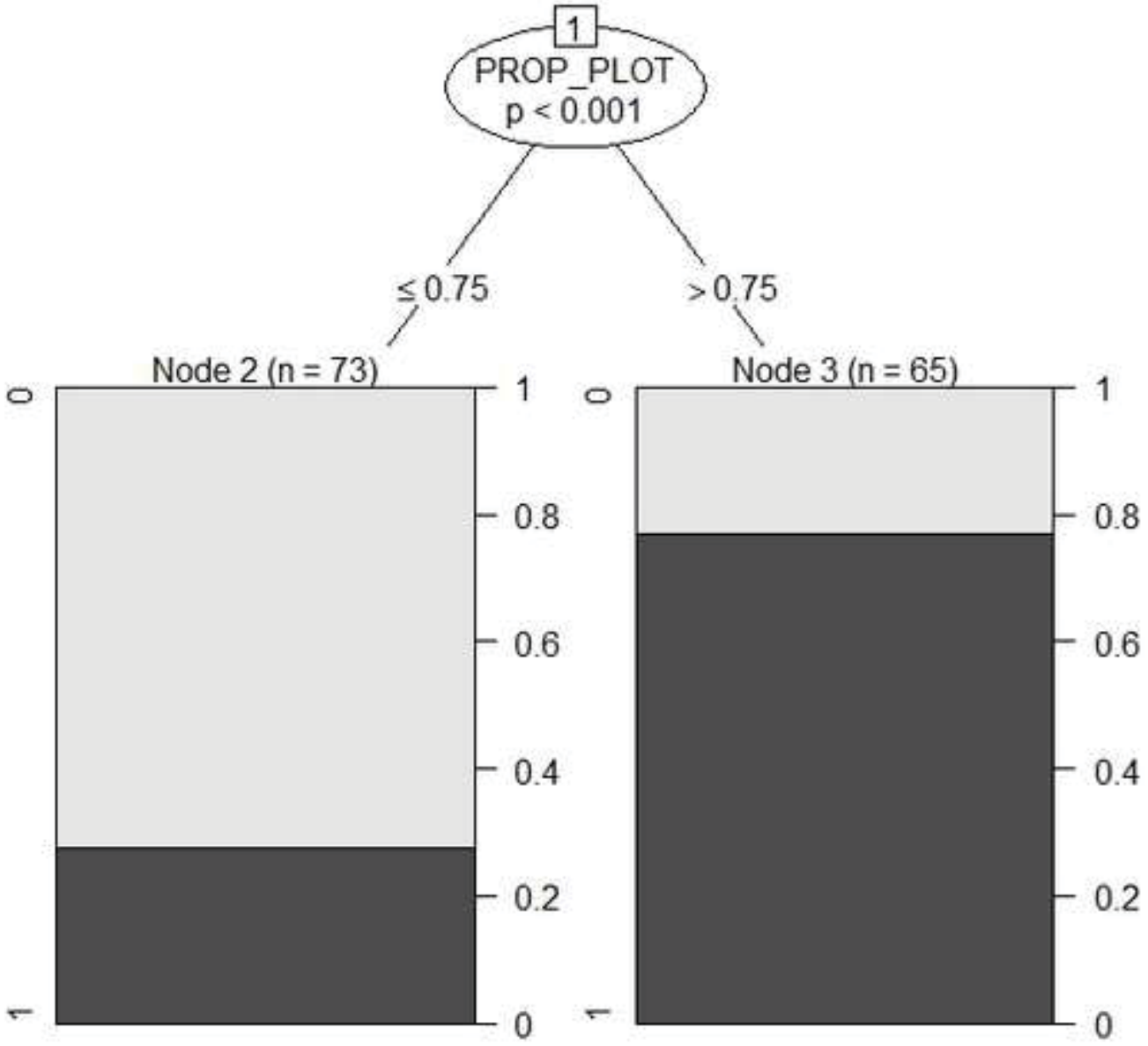

Supplementary material

Click here to download Supplementary material: Appendix A.docx